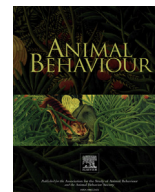




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Culture and cultural evolution in birds: a review of the evidence

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Social learning from the observation of knowledgeable individuals can allow behaviours, skills and techniques to spread across populations and transmit between generations, potentially leading to emergent cultures. An increasing body of research has not only evidenced the occurrence of cultural behaviour in nonhuman animals, but also hypothesized that such cultures could 'evolve' over time in a way that shares key characteristics with biological evolution, including through a process of selection on variance, inheritance and adaptation. Outside of humans, song and contact calls in birds provide by far the most comprehensive evidence for culture and cultural evolution. However, birds have often been considered 'one-trick cultural ponies', only exhibiting significant diversity in this single component of their behavioural repertoire. Recent studies have begun to challenge this view. Here, I review the evidence across multiple behavioural domains for wild cultures in birds. I then discuss the evidence in birds for four key concepts of cultural evolution: (1) variation, selection, inheritance, (2) adaptation, (3) geographical and demographic processes and (4) the accumulation of modifications. I incorporate the evidence from birdsong with other behavioural domains for each key concept and identify important gaps in knowledge. Finally, I discuss how taking a cultural evolution perspective can be informative for our understanding of cognitive ecology more broadly.

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Learning is a vital form of behavioural plasticity that allows individuals both to fine-tune their behaviour to local environmental conditions (Snell-Rood, 2013) and to increase their behavioural repertoire through the introduction of new information (Dukas, 2013). When this learning occurs socially (from the observation of, or interaction with, others), there is the additional potential for behaviours to be transmitted across many individuals and at broad scales, including across populations and over generations (Heyes & Galef, 1996). This flow of information, behaviour, skills or techniques between individuals is a fundamental process in animal ecology: social learning enables individuals to exploit the previous experience of others to improve individual fitness (Slagsvold & Wiebe, 2011). It thus may act as a mechanism by which individuals could exhibit local adaptive behaviour (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). Over short timescales, the social transmission of behaviour can lead to the diffusion of new innovations through populations, for example of song types (Garland et al., 2011) or foraging techniques (Allen, Weinrich, Hoppitt, & Rendell, 2013; Aplin et al., 2015a, 2015b; Kawai, 1965).

Over longer timescales, social learning could potentially also lead to the formation of local cultures (Aplin, 2016; Laland & Hoppitt, 2003; Laland & Janik, 2006; Whitehead, Rendell, Osborne, & Wursig, 2004; Whiten, 2011), and even could function as a 'second inheritance system' to genetic evolution; while vital in humans (Boyd & Richerson, 1985; Boyd, Richerson, & Henrich, 2011; Mesoudi, 2015), the importance of this in other animals has only just begun to be investigated (Laland & Rendell, 2013; Whiten, 2005, 2017b; Whiten, Hinde, Laland, & Stringer, 2011).

Social learning can thus theoretically lead to the emergence of traditions and culture, wherein groups or populations share distinctive behaviours that are persistent over time and maintained via the social transmission of behaviour within and between generations (Laland & Janik, 2006; Rendell & Whitehead, 2001; Whiten, Ayala, Feldman, & Laland, 2017). Once established in a population, such cultures can also potentially be extremely stable, persisting over centuries (for example in yellowhammer song, *Emberiza citrinella*; Pipek et al., 2017), or possibly even over thousands of years, as suggested by archaeological evidence of stone tool use in chimpanzees, *Pan troglodytes* (Haslam et al., 2009; Luncz, Wittig, & Boesch, 2015; Mercader, 2007). However, cultures are not necessarily completely static: over time their component traits can change, altering in form, function or frequency. Multiple parallels have been drawn between this process and Darwinian

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genetic evolution, with some authors proposing that (1) culture may also be under selection and ‘evolve’, and (2) the process by which this occurs can be described using concepts and methods borrowed from biological evolution (Mesoudi, 2015, 2017; Whiten et al., 2011).

Such a theory of ‘cultural evolution’ is an area of active study in evolutionary anthropology and human sociobiology (Henrich, Boyd, & Richerson, 2008; Mesoudi, 2015, 2017; Whiten et al., 2017), where authors have suggested that cultural traits in humans may show multiple parallels to the core principles of genetic evolution, including being subject to variation, selection and inheritance; adaptation; geographical variation, migration and drift; and the accumulations of modifications or changes in function (Mesoudi, 2017). However, these ideas have also been raised in relation to nonhuman animals for several decades (Aval & Jablonka, 2000; Galef, 1976; Mundinger, 1980), and while controversial, have gained traction in the birdsong literature in particular (e.g. see discussions on the role of geographical variation and social movement on birdsong, Podos & Warren, 2007). Outside of birdsong, ideas of a general theory of cultural evolution are only now beginning to be discussed in the nonhuman animal literature, helped by a growing body of evidence and increasingly sophisticated experimental approaches (e.g. Whiten, 2017a, 2017b).

The strongest evidence for animal cultures across broad behavioural domains has largely come from two groups, the primates (Whiten, 2017a) and the cetaceans (Rendell & Whitehead, 2001); for a comparison, see Botting, van de Waal, and Rendell (2017). By contrast, despite providing by far the best evidence for vocal cultures, birds have often been thought as ‘one-trick ponies’, only exhibiting significant diversity in this single component of their behavioural repertoire (Whiten et al., 2017). To some extent this has led to an exclusion of birdsong from discussions about the evolution and ecology of culture, as well as a possible lack of consideration of social learning observed in other behavioural domains (Aplin, 2016). I would argue that recent evidence suggests that this view needs rethinking. Here, I review this evidence for culture in different bird species across multiple behavioural domains. I then discuss the evidence from both the birdsong literature and other behavioural domains for cultural evolution and identify important gaps in our knowledge (Table 1). I finish by discussing the wider implications of this research topic for cognitive ecology more broadly.

ANIMAL CULTURE

Social learning appears to be taxonomically widespread (Heyes, 2012) and utilized by individuals across diverse contexts (Aplin, 2016); for example in birds, the use of social learning ranges from predator recognition (European blackbird, *Turdus merula*: Curio, Ernst, & Vieth, 1978) to courtship (Japanese quail, *Coturnix japonica*: White, 2004) and foraging (European oystercatcher, *Haematopus ostralegus*: Norton Griffiths, 1967). However, emergent cultures are much less well documented in animals and appear to be rare and more taxonomically restricted. Perhaps most famously, a large body of evidence has been collated in chimpanzees to show that populations across Africa differ in their behaviour in multiple domains, from tool use techniques to grooming practices (Biro et al., 2003; Hopper et al., 2007; Whiten, 2005, 2011; Whiten et al., 1999). Many of these population or group-specific behaviours appear to have no obvious environmental correlates (Whiten et al., 1999), and some even appear to have a very long history of use, uncovered with ‘primate archaeology’ (Luncz et al., 2015). Likewise, extensive behavioural observations in wild orang-utans, *Pongo pongo*, have revealed cultural variation in behaviour across

subpopulations, for example in their communication and tool use (van Schaik, Marshall, & Wich, 2009; van Schaik et al., 2003).

In birds, similarly, there has been a long history of study showing that song can differ between populations and groups, forming local ‘dialects’ (Slater, 2003). This extensive body of research has demonstrated that vocalizations (particularly in the passerines and parrots) are also often at least partly socially learnt from parents or conspecifics, either in early developmental periods or throughout life (Beecher & Brenowitz, 2005; Marler, 1970; Nottebohm, 1970; Slater, 1986). Social transmission, combined with population structure (e.g. Fayet, Tobias, Hintzen, & Seddon, 2014), geographical variability (e.g. Keighley, Langmore, Zdenek, & Heinsohn, 2017), assortative mating (e.g. Freeberg, 1996; Grant & Grant, 1996) and/or conformity (Bartlett & Slater, 1999; Lachlan, Janik, & Slater, 2004) can then lead to distinct and long-lasting regional cultures in song structure and composition (Slabbekoorn & Smith, 2002). While most research has been conducted on male song in passerines, regional dialects can also occur in other types of vocalizations. For example, in parrots, regional and roost site dialects have been noted in contact calls (Baker, 2000; Bradbury, Cortopassi, & Clemmons, 2001; Wright & Dahlin, 2018; Wright, 1996). In laboratory experiments, groups of parrots will also converge on shared calls, with immigrants adopting the vocalizations of groups they move into (Bartlett & Slater, 1999). Overall, this literature is extremely extensive and cannot be fully reviewed here; however, see recent reviews on birdsong, including Beecher and Brenowitz (2005), Catchpole and Slater (2003), Podos and Warren (2007), Slabbekoorn and Smith (2002) and Slater (2003).

Outside of vocalizations, the best candidates for cultures in birds are observed in localized foraging behaviours. Indeed, the first potential cultural transmission of a foraging behaviour in birds was noted as early as 1921, when tits (great tit, *Parus major*; blue tit, *Cyanistes caeruleus*) were observed piercing the foil caps of milk bottles left on door-steps in southwest Britain, in order to eat the cream (Fisher & Hinde, 1949). This behaviour was recorded increasingly often and across an increasingly wide geographical area, and persisted for more than 20 years (Fisher & Hinde, 1949; Hinde & Fisher, 1951, 1972). This led to the suggestion that this innovation had spread and established to form a new culture (Lefebvre, 1995). While the underlying learning mechanisms were challenged in later captive experiments (Kothbauer-Hellman, 1990; Sherry & Galef, 1984, 1990), recent studies have provided experimental evidence in captivity (Aplin, Sheldon, & Morand-Ferron, 2013) and in the wild (Aplin et al., 2015a, 2015b) to demonstrate that these species can socially learn new foraging techniques and can transmit novel behaviours through social networks that will then go on to establish and persist as stable traditions. Since 1921, multiple such innovations in foraging behaviour have been noted in different populations of tits, for example, one subpopulation of tits in Hungary has been recorded eating hibernating pipistrelle bats in a cave for over more than 10 years (Estok, Zsebok, & Siemers, 2010). While mechanisms for the persistence of these innovations in populations have not been explicitly tested, given that research has suggested that much of the foraging niche in this species is socially learnt (Slagsvold & Wiebe, 2007, 2011), it seems highly likely that they could be socially transmitted and culturally inherited.

Another interesting example of a foraging innovation that appears to be both locally adaptive and actively spreading occurs in one population of kelp gulls, *Larus dominicanus*, at Peninsula Valdés, Argentina. Here, kelp gulls were first observed tearing skin and blubber from the backs of resting southern right whales in the 1970s, a behaviour that, while not fatal, can be highly detrimental to the whales. While individual gulls were not followed, aerial survey photographs taken during 1974–2011 showed an increase in

Table 1

Glossary of terms used in the text, with examples of analogous processes in genetic evolution and examples of empirical evidence

Term	Definition	Analogous processes	Empirical examples
Animal culture	Behaviour that is socially learnt and acquired, shared by members of a group or community and persistent over time (Laland & Janik, 2006)		Different subpopulation preferences for foraging techniques in parids (experimentally induced: Aplin et al., 2015a, 2015b) and New Caledonian crows (Hunt & Gray, 2003)
Cultural inheritance	Information transmitted from previous generations. Can form a potentially important part of individuals' behavioural repertoire, when it is often referred to as a 'second inheritance system' (Whiten, 2005)	Inheritance of genes ('primary inheritance system')	Experiments cross-fostering chicks of two parid species into heterospecific nests revealed that song and foraging behaviour are partly socially acquired from older individuals (Slagsvold & Wiebe, 2007)
Cultural evolution	Darwinian theory of cultural change (Mesoudi, 2017)	Genetic evolution	Long history of research into factors underlying temporal and spatial change in song dialects (Slater, 2003)
Variation	Process creating variability in traits, including innovation and copying errors	Genetic mutation and recombination	'Cultural mutation rates' estimated in song learning by chaffinches (e.g. Lachlan & Slater, 2003)
Selection	Forces acting on cultural traits to change their frequency in the population	Natural selection and sexual selection	Social learning biases for the majority behaviour observed in foraging behaviour in parids (Aplin et al., 2015b, 2015a) and in vocal learning of contact calls in parrots (Bartlett & Slater, 1999)
Adaptation	The process by which cultural behaviour becomes refined in response to the physical or social environment	Dynamic evolutionary process whereby traits are selected for that enhance fitness	Innovations spread and persist that provide access to a new food resource, e.g. pecking whale blubber in kelp gulls (Marón et al., 2015), opening milk bottles in parids (Fisher & Hinde, 1949)
Geographical processes	Geographical and demographic factors that contribute to changes in cultural trait frequencies in populations, e.g. migration rates	Similar processes leading to genetic change with geographical distance, e.g. gene flow, founder effects	Song of chaffinches colonizing an island chain shows reduced complexity with progressive colonization events (Lachlan et al., 2013)
Drift	Neutral changes over time in cultural trait frequencies in isolated subpopulations	Genetic drift	Divergent song types in isolated and fragmented populations, e.g. in North Island saddlebacks (Parker, Anderson, Jenkins, & Brunton, 2012)
Cumulative culture	Cumulative build-up of complexity in cultural behaviour over generations, leading to cultural traits that 'no one individual could have invented in their lifetime'	Accumulation of modifications in biological evolution, leading to complex adaptive outcomes, e.g. the eye	No clear examples in birds. Has been suggested for over-generational increases in complexity in song (Feher, Wang, Saar, Mitra & Tchernichovski, 2009) and for 'stepped tool types' in New Caledonian crows (Hunt & Gray, 2003)

whales with gull lesions from 2% to 99%, suggesting that the behaviour had spread and persisted throughout the gull population (Marón et al., 2015). Except for two isolated incidents, this behaviour has not been observed at any other site, suggesting that it may form a local culture. Interestingly, and perhaps related to learned avoidance behaviours by adult whales (Fazio, Argüelles, & Bertellotti, 2014), there has also been a shift in the behaviour in over time, with the focus of attacks moving from adult mothers (which largely received the majority of attacks in 1988; Thomas, 1988) to calves (which were the focus of 69% of attacks in 2011; Marón et al., 2015).

Cultural explanations have also been proposed for geographical variation in foraging tools in New Caledonian crows, *Corvus moneduloides*. In Hunt and Gray (2003), the authors proposed that geographical variation in tool manufacture across the New Caledonian crow population was evidence of the presence of local 'tool-type' cultures. This was challenged by work showing that juvenile crows will spontaneously use tools in isolation (Kenward, Weir, Rutz, & Kacelnik, 2005), although social learning and the opportunity to handle previously used tools from experienced adults also clearly influences behavioural development (Kenward, Rutz, Weir, & Kacelnik, 2006; Logan, Breen, Taylor, Gray, & Hoppitt, 2016). It has also since been suggested that the observed geographical variation in tool types may be a result of young individuals copying

the physical form of discarded tools of local adults (Logan et al., 2016). This species has traditionally been difficult to observe in the wild, and so much remains to be discovered about how variability in tool use relates to genetic, environmental and social factors; although promising new remote-tracking technologies give the possibility that this research may soon be feasible (Rutz, Bluff, Weir, & Kacelnik, 2007; Rutz, Burns, et al., 2012). Yet, in any case, while the exact mechanisms underlying the differences in tool use in different areas of the island are still to be proven, this remains one of the most well-known examples of bird culture.

Finally, two intriguing examples show how culture may occur across diverse behavioural contexts. First, many bird species migrate in family or social groups (e.g. geese and cranes), and it has long been postulated that for these species, social learning from experienced individuals may be a vital factor shaping route choice in naïve juveniles (Kao et al., 2018). This was demonstrated in whooping cranes, *Grus americana*, where the presence of experienced older individuals in migratory flocks increased the long-term accuracy of migration for less experienced individuals, with the highest benefits accrued from learning from very old birds (Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013). In a study on European bustards, *Otis tarda*, Palacín, Alonso, Alonso, Magaña, and Martín (2011) additionally highlighted the interaction between cultural transmission and social structure, finding that the opportunity to

travel in family units allowed for the cultural inheritance of migration patterns from mother to daughter, while in immature males, migratory behaviour was instead shaped by the social transmission of information from adult males within single-sex flocks.

Second, Madden and colleagues (Madden, 2008; Madden, Lowe, Fuller, Dasmahapatra, & Coe, 2004) have proposed that bowerbirds may potentially exhibit local cultures in their bower structure and displays. While more work needs to be undertaken on learning mechanisms, males appear to take several years to acquire proficiency in bower construction and in mating displays. During this time, multiple studies have observed that immature males will regularly make investigatory visits to active bowers, where they have the opportunity to acquire knowledge about the structure, display and vocalizations of breeding adults (studies summarized in Madden, 2008). Populations differ in bower design and decorations (Diamond, 1982, 1986, 1987), and at least at one site (Madden et al., 2004), bowers that were spatially close by exhibited similar decorations, a pattern unrelated to the total availability of decorations in the environment.

CULTURAL EVOLUTION IN BIRDS

Although research is still in early stages, these examples demonstrate that candidate traditions and cultures can be identified across multiple taxa of birds, and in multiple behavioural contexts. As noted above, cultural evolution theory would further suggest that these traditions are not necessarily static, but may also ‘evolve’ over time. Indeed, there are multiple parallels that can be drawn between the way in which cultural traits can persist or change and genetic evolution (Table 1). For example, dispersal allows both genes and learnt behaviours to move between populations, while innovations and errors in copying introduce new variants, similar to genetic mutations. However, there are also fundamental differences between genetic and cultural evolution that are important to consider. First and foremost, cultural variants are often transmitted both horizontally (within generations) and vertically (between generations). Second, what are transmitted are often not discrete units between two individuals: behaviours can blend together, be transmitted from one to many or rapidly change within a single generation. Third, cultural traits can interact with individual cognition, for example some individuals or species may not be able to copy units of information with high fidelity. The capacity of individuals to acquire behaviour may also be restricted to certain development stages (Slater, 2003) or can vary with environment and state (Aplin et al., 2013; Roth, LaDage, & Pravosudov, 2010). Individuals acquiring behaviour may also choose not to express it (Drea & Wallen, 1999), or potentially modify it with individual practice (Madden, 2008). That said, and despite these fundamental differences, Darwin’s core principles can all likewise be usefully applied to the process of cultural evolution, including: variation, selection, inheritance, adaptation, geographical variation and the accumulations of modifications. Below I assess the applicability and evidence for each of these in birds.

Variation, Selection and Inheritance

Variation, selection and inheritance are core tenets of Darwinian evolution, with genetic variation introduced via processes of mutation and recombination, selection through differences in survival and reproduction and inheritance through the vertical transmission of traits. In theories of cultural evolution, they are likewise central: variation in traits is introduced by copying errors or innovations, and selection on this variation can occur, for example, through transmission biases and/or the interaction between

individual experience and social learning. Ultimately, the inheritance of information is then via general patterns of social learning within and between generations (Mesoudi, 2015). In birds, there is evidence that cultural behaviour undergoes all of these processes.

Studies in birdsong suggest that vocalizations may often be copied with some error, although there are contrasting estimates of the extent of these copying errors and their potential importance in introducing new variants. For example, two empirical studies in chaffinches, *Fringilla coelebs*, suggested that the ‘cultural mutation rate’ (the proportion of songs learnt inaccurately, leading to novel song types) might be as low as 1–2% (Lachlan & Slater, 2003) or as high as 10–15% (Slater, 1986; Slater, Ince, & Colgan, 1980). There is also evidence from many bird species that individual-level innovations can potentially introduce behavioural variation into populations (Overington, Cauchard, Cote, & Lefebvre, 2011; Reader & Laland, 2003). For example, as detailed above, multiple instances of innovative behaviour have been recorded in one species, the great tit (Cole, Cram, & Quinn, 2011), some of which appear to have spread to form new traditions (Lefebvre & Aplin, 2017). What predicts such behavioural flexibility and innovativeness is an active research area that cannot be comprehensively summarized here (see Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Quinn, Cole, Reed, & Morand-Ferron, 2016; Reader & Laland, 2003; Reader, Morand-Ferron, & Flynn, 2016). However, even if innovations events are rare, they can potentially be an important source of new cultural variants. Perhaps uniquely to cultural evolution, the diffusion of innovations can lead to big jumps and major transitions in behaviour, for example potentially providing the means to invade new habitats or exploit new niches (Aplin, 2016; Slagsvold & Wiebe, 2007).

Once variation exists in cultural traits, this can be selected on by users, changing trait frequencies and their persistence. The most fundamental way in which selection operates on cultural variants is likely to be through social learning biases. Indeed, there is a long history of theoretical and empirical research to show that individuals often do not copy randomly, but rather use social learning strategically, optimizing their learning outcomes by utilizing ‘short cut’ rules to determine when, how and what to copy (Laland, 2004; Rendell et al., 2011). For example, great tits exhibit a conformist bias, where an individual preference to adopt the majority behaviour leads to the dominance of the most frequent foraging technique (Aplin, Sheldon, & McElreath, 2017; Aplin et al., 2015a, 2015b). In song learning, content biases appear to play a particularly important role in transmission dynamics, e.g. some bird species prefer to copy songs that resemble those of conspecifics, suggesting that they have a bias towards a particular acoustic template (Braaten & Reynolds, 1999; Grant & Grant, 1996; Nelson, 2000a; Slabbekoorn & Smith, 2002).

However there are a variety of other ways in which cultural variants could be under selection. For example, variants could be shaped over time by an interaction with individual learning, either through overproduction and selective retention, or through a feedback with individual experience. There is good evidence for the first of these mechanisms in passerine song, with several studies suggesting that this learning method may affect the rate of cultural evolution of song types (Marler & Peters, 1982; Peters & Nowicki, 2017). In field sparrows, *Spizella pusilla*, and white-crowned sparrows, *Zonotrichia leucophrys*, males selectively retain the songs of their neighbours, leading to the local clustering of song types (Nelson, 1992, 2000b). This learning bias may be particularly important in maintaining dialect differences in contact zones (Nelson & Marler, 1994; Nelson, 2000b). The best evidence for the second mechanism comes from an experimental study on homing pigeons, *Columba livia*. Here, individuals were paired/re-paired in a transmission chain experiment that simulated generations. When

repeatedly flying a route between two points, the contribution of small modifications by multiple different individuals led to progressive improvements in the efficiency of the socially learned route (Sasaki & Biro, 2017). This may be the mechanism by which migratory routes develop over time, via an interplay between collective navigation and cultural inheritance (Kao et al., 2018).

Inheritance is inherent in all examples of social learning and culture as given above, as the behaviour is transmitted from individual to individual. However, when considering the evolution and ecology of culture, evidence that information can carry over multiple generations is particularly important. Again, there is good evidence for this in birds. Some song types can be transmitted from father to son and within local communities over decades or even centuries (Baker & Thompson, 1985; Pipek et al., 2017). In parids, cross-fostering experiments have revealed that juveniles acquire much of their foraging niche from social interactions with older individuals (Slagsvold & Wiebe, 2007), while my previous work gave experimental evidence for the transmission of a novel foraging technique over two generations (Aplin et al., 2015a, 2015b). Yet unlike in other taxa (e.g. primates), evidence for the vertical transmission of foraging behaviour from parent to offspring during juvenile development is relatively rare, with most studies indicating oblique transmission (from older to younger individuals). More research therefore needs to be undertaken to investigate patterns of cultural inheritance in species with extended periods of parental care.

Adaptation

That culture has adaptive value is fundamental to the idea of cultural evolution in humans and is often tied to the idea of social conventions and tribalism (Henrich & McElreath, 2003). Some of these concepts have also been extended to other animals, for example in whales, where it has been argued that group-specific vocalizations might act as 'symbolic marking', facilitating group cooperation and cohesion (Cantor et al., 2015). In general, however, culture is more likely to have adaptive significance through the provision of behavioural tools to novel problems, which are then refined over time through an interaction between variation, selection and inheritance, and the environment. For example, it has been argued that in primates, tool use traditions may allow individuals and groups to persist in harsh periods when the food gained through these techniques becomes a more significant part of overall diet (Yamakoshi, 1998). Similarly, food obtained through stick tool use forms a vital part of the diet of New Caledonian crows and may be partly socially learnt (Rutz et al., 2010). In birds, foraging innovations that have spread and persisted are likely to have done so because they represent locally adaptive behaviour, for example the 'milk bottle innovation' in tits allowed individuals to access a new food resource (Fisher & Hinde, 1949). However, vitally, no study has yet successfully linked the presence of a culturally transmitted and inherited behaviour with improved survival or reproduction.

In birdsong, it has been suggested that cultural evolution could assist with urban adaptation. Much of the adaptive response to traffic noise in birds has been shown to be the result of individual plasticity. However, cultural processes may also contribute (Zollinger, Slater, Nemeth, & Brumm, 2017). For example, in a study on white-crowned sparrows in San Francisco over 30 years, Luther and Baptista (2010) documented a rise in the minimum frequency of song types over multiple generations, an effect that the authors suggested might be attributable to ambient noise favouring the cultural transmission of higher-frequency songs.

Interestingly, it also remains an open question as to whether culture is always or even usually adaptive (Galef, 1995; Laland, 1996). Some authors have argued that culture may actually allow

for suboptimal or even harmful behaviours to persist in populations, if individuals continue to copy out-of-date or inappropriate information (Kendal, Coolen, van Bergen, & Laland, 2005; Laland & Williams, 1998). In this case, social learning strategies such as conformity may even facilitate the perpetuation of outdated behaviour, as individuals are using an indirect measure of information quality (in this case, the majority choice). However, as yet, there is no evidence for this in birds. On the contrary, in the one experiment to look at this question, populations of great tits were able to flexibly adjust stable traditions to a new optimum after a change in resource payoffs (Aplin et al., 2017). This was achieved through a combination of conformist social learning with payoff-sensitive individual reinforcement. That is, the results suggested that as long as some variation in behaviour exists among individuals and there is some social mixing, all variants will eventually be socially learnt by some other individuals. As individuals reliably perform the best behaviour in their repertoire (Rendell et al., 2010), this enables the best cultural trait to be repeated and propagate through the population (Aplin et al., 2017).

Geography, Demography, Neutral Processes

It is well accepted that geographical and demographic factors such as population connectivity, spatial distribution and population size are vital contributors to evolutionary change in species. These are all also thought to represent crucial processes in cultural evolution. For instance, traditions may diverge through drift-like processes when populations are isolated, as argued for chimpanzee cultures (Whiten et al., 1999). In birds, passerine song has provided the strongest evidence outside of humans on the effect of spatial distributions and geographical isolation on the form and frequency of cultural traits. For example, yellowhammers introduced to New Zealand appear to have preserved old dialects now extinct in their native British range (Pipek et al., 2017), and songs of birds on islands show evidence of founder effects, with reduced complexity and diversity (Baker, 1996; Baker, Baker, & Tilghman, 2006; Parker, Anderson, Jenkins, & Brunton, 2012). Invasive chaffinches have proved a particularly good test of these processes: on the Chatham Islands, which chaffinches colonized around 1900, the basic song structure has remained largely unchanged, and unlike their mainland relatives, birds have not developed elaborate end phrases to their song (Baker & Jenkins, 1987). Moreover, in their sequential colonization of the Atlantic islands, chaffinches appear to have experienced a progressive loss of syntactical structure with each colonization event (Lachlan et al., 2013).

Within populations, theoretical modelling suggests that movement rates are also likely to play a role influencing the form, frequency and longevity of cultural traits (Nunn, Thrall, Bartz, Dasgupta, & Boesch, 2009), and that social structure will be an important predictor of cultural diversity and complexity (Dereck & Boyd, 2016). One example of this occurs in one woodland population of great tits (Fayet et al., 2014), where song repertoire size of neighbourhoods was correlated with levels of immigration, but song diversity declined with increasing movement rates (also see Laiolo & Tella, 2007; Rivera-Gutierrez, Matthysen, Adriaensen, & Slabbekoorn, 2010). However, importantly, biased transmission mechanisms can additionally influence or mask this effect. For instance, cultural conformity will make group traditions resistant to erosion from incoming cultural variants (Lachlan et al., 2004; Whiten, Horner, & de Waal, 2005). In one laboratory experiment in budgerigars, *Melopsittacus undulatus*, Bartlett and Slater (1999) found that immigrating individuals will change their contact calls to match the group, while the majority behaviour does not change. Similarly, after an experimental introduction of new foraging behaviours to multiple subpopulations of great tits, birds immigrating between

experimental patches with different traditions tended to change their behaviour to match the local majority (Aplin et al., 2015a, 2015b), and thus also had no impact on the patterning of cultural diversity.

Accumulation of Modifications

Ultimately, biological evolution is characterized by a successive series of small modifications that can lead to complex adaptive outcomes. Likewise, cultures in humans have ratcheted over time through the interaction between innovation and social learning, eventually leading to outcomes as complex and astounding as space flight, skyscrapers, or a theory of mathematics (Boyd et al., 2011; Carruthers, 2013; Mesoudi, 2017). Of all cultural evolutionary processes, this cumulative culture has attracted the most attention; extensive research effort has focused on understanding how humans have evolved such unique cultural capabilities (Henrich, 2015; Lewis & Laland, 2012). In particular, whether any other species exhibit basic forms of cumulative culture is an area of active and intense debate (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Deffuant, Huet, & Amblard, 2005; Whiten, 2005). While most of this debate has been focused on nonhuman primates (e.g. tool use in chimpanzees, Whiten, 2017a), two studies in birds have examined whether socially learnt behaviours can increase in complexity over time. First, in Feher et al. (2009), the authors experimentally raised captive zebra finches, *Taeniopygia guttata*, in complete acoustic isolation, before allowing them to breed in colonies. Initially, founding birds sang a garbled isolate song, but over four generations the song evolved towards the more complex wild type, undergoing a progressive accumulation of alterations from each generation.

Second, Hunt and Gray (2003, 2006) argued that the presence of multistep pandanus tools in New Caledonian crow populations was highly suggestive of cumulative culture. These tools are more complex to manufacture than straight tools, and arguably more efficient to use (Hunt & Gray, 2006). The authors also found geographical variation in the distribution of these tools, with the use of straight tools restricted to one end of Grande Terre Island. The evidence since this study for this proposition has been mixed. There is opportunity for cultural inheritance; young birds take several years to acquire proficiency in tool use and appear to gain information on tool manufacture from handling adult tools and from observation (Bluff, Troschianko, Weir, Kacelnik, & Rutz, 2010; Logan et al., 2016). However, there is no conclusive evidence that stepped tools represent a true advance on other tool types. Additionally, although these are not mutually exclusive explanations, tool use in this species is likely the result of the interplay of several factors, including genetic and ecological influences (Kenward et al., 2006, 2011; Klump, Sugawara, St Clair, & Rutz, 2015; Rutz, Ryder, & Fleischer, 2012). While obviously bird cultures do not show the complexity and diversity seen in human cumulative culture, these two studies, as well as emerging evidence from collective navigation (see above; Kao et al., 2018; Sasaki & Biro, 2017) suggest that much more remains to be discovered about the way in which cultural traits can be refined or improved over time.

WHY CARE ABOUT CULTURE IN BIRDS?

Social learning is a fundamental component of animal cognitive ecology (Aplin, 2016; Galef & Giraldeau, 2001; Seppänen, 2007; Slagsvold & Wiebe, 2011). It is a potentially important means by which social animals, including many bird species, learn their ecological niche (Slagsvold & Wiebe, 2007), interact with conspecifics and heterospecifics (Seppänen, 2007; Slabbekoorn & Smith,

2002) and exhibit behavioural flexibility (Dukas, 2013; Snell-Rood, 2013). As the examples given above demonstrate, there is increasing evidence that the social learning and sharing of information within groups may lead to the formation of traditions, such as in birdsong dialects or subpopulation-specific foraging techniques. But do such emergent cultures matter for cognitive ecology, or are they merely a curiosity of behaviour?

First, studies on social learning have often focused on how and when individuals use such learning, with the implicit assumption that information is available to be acquired. Taking a 'cultural perspective' allows researchers to examine the link between an individual's learning experience and population-level processes; for example, by asking how the opportunity to learn that particular information has been shaped by population structure, composition or size (Aplin et al., 2015a, 2015b; Cantor & Whitehead, 2013). Taking a 'cultural evolution perspective' broadens the questions still further, allowing researchers to use contemporary behavioural patterns to speculate about what historical factors might have shaped the availability of information, or to ask how individuals in different populations might experience different learning opportunities. Finally, it allows the researcher to track the interactions between socially learning individuals and the population over time, for example, by examining how individual experience and culture feedback to further refine population-level behaviour (Kao et al., 2018).

Second, the cultural inheritance of information allows for the transfer of information or behaviour between generations, and this 'second inheritance system' can potentially extend the scope of biology (Creanza, Kolodny, & Feldman, 2017; Whiten, 2017b). This second inheritance system might even directly interact with genetic evolution; through gene–culture coevolution (Whitehead, 2017), through the speciation of 'culturally isolated' populations (Slabbekoorn & Smith, 2002), or through selection on individuals to most efficiently exploit this information (Boyd et al., 2011), see the 'cultural intelligence hypothesis: Street, Navarrete, Reader, and Laland (2017). Culture and cultural evolution will further make this transfer of inherited behaviour locally adaptive, via the selection and refinement of learnt behaviour within and between generations (Galef, 1995; Sasaki & Biro, 2017). Over the short term, this might be one way in which some social animals could exhibit adaptive behavioural responses to novel challenges and new opportunities, through the horizontal spread and vertical inheritance of new beneficial innovations.

SUMMARY

Studies on vocalizations in birds have provided some of the most comprehensive examinations of cultural evolution. In particular, the birdsong literature has been pioneering in integrating genetic, environmental and cultural explanations for behaviour and in considering how interactions between these might influence evolutionary and ecological outcomes (Laland & Janik, 2006). Yet, in broader discussions of the evolution of animal culture, birds have traditionally been excluded as 'one trick cultural ponies'. Conversely, while research in birds has been central to the development of the field of behavioural ecology, cultural explanations have often been neglected when considering hypotheses for variation in, and ontogeny of, other forms of behaviour. While still early and exploratory, recent evidence is challenging this view, with exciting developments in the study of culture and cultural evolution across multiple behavioural domains, from migration to tool use. Future work in animal cognition should continue to explore these possibilities and take advantage of new technologies to experimentally manipulate behaviour *in situ* to test hypotheses arising out of this emerging theoretical framework.

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